

A new genus and species of hermit crab (Decapoda: Anomura: Paguridae) from seamounts off south-eastern Tasmania, Australia

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Abstract

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A new and highly variable species, representing a new genus of hermit crabs, is described and illustrated. In addition to the morphological changes in shape and armature of the chelipeds associated with growth in *Bythiopagurus macrocolus*, gen. nov., sp. nov., this species exhibits a singular development of the left chela that may be an adaptation to its specialised habitat among colonies of the stony coral *Solenosmilia variabilis* Duncan. The similarities seen among the genera *Bythiopagurus*, gen. nov., *Michelopagurus* McLaughlin and *Icelopagurus* McLaughlin appear to be superficial and convergent; *Bythiopagurus* appears phylogenetically related to the *Pylopaguropsis* group of genera characterised by 13 pairs of bi- or quadriserial gills.

Key words

Crustacea, Anomura, Paguridae, new genus, new species, Tasmania, seamounts, *Bythiopagurus*

Introduction

The seamount region of south-eastern Tasmania is a distinctive deep-water environment extensively surveyed for the first time between 20 January and 1 February 1997. Among the approximately 242 species of invertebrates cited by Koslow and Gowlett-Holmes (1998) in their report on the survey, only three were hermit crabs. Two of the three were new to science. *Propagurus dep profundis* (Stebbing, 1924), described initially from South Africa, was reported by McLaughlin and de Saint Laurent (1998) to range from South Africa to Hawaii, and had been collected previously in Tasmanian waters (McLaughlin, unpub.). Of the latter two, the species of *Goreopagurus* described by Lemaitre and McLaughlin (2003) is the first truly deep-water record (620–1300 m) for this genus, and the first report of the genus outside the continental waters of Atlantic and Pacific coasts of the United States. The unusual species reported herein represents both a new species and a new genus that is noteworthy not only for its characteristic growth-related variability, but for its unusual habitat. It was found only in association with colonies of the stony coral, *Solenosmilia variabilis* Duncan, 1873.

Measurements include shield length, measured from the tip of the rostrum to the midpoint of the posterior margin of the shield. However, in this genus, as in a few others, e.g. *Goreopagurus* McLaughlin, 1988, *Alainopaguroides* McLaughlin, 1997, the shield breadth: length ratio increases appreciably with increased animal size, thus making the

measurement of shield length less informative than for most pagurid genera. The ratio was calculated of corneal diameter (maximum measured width of the left cornea) to length of the ocular peduncle (length of the left ultimate peduncular segment, including the cornea, along the lateral surface). Male sexual tube development varies from a simple papilla-like protrusion to very short (less than coxal length) tube(s), but occasionally the vas deferens may not be extruded at all. The holotype and most paratypes are deposited in Museum Victoria, Melbourne, Australia (NMV); and three paratypes in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Terminology. For the most part, the terminology utilised in the species description follows that of McLaughlin (1997) but the interpretation of gill structure is based on the definition of Lemaitre (in press). The varying extent to which the paguroid cephalothorax is delineated and/or calcified has resulted in a certain amount of confusion regarding the correct terminology to be applied to various portions (e.g. Boas, 1880, 1926; Bouvier, 1895; Borradaile, 1906; Jackson, 1913; Pilgrim, 1973; McLaughlin, 1974; Forest, 1987). Morgan and Forest (1991) corrected the misinterpretation by McLaughlin (1974) regarding the sulcus cardiobranchialis and assigned the name cardiac sulci to the previously unnamed sulci bordering the postero-medial plate. Lemaitre (1995) added another term “accessory portion” for the calcified portion of the carapace presumably delineated anteriorly by the cervical groove and posteriorly by

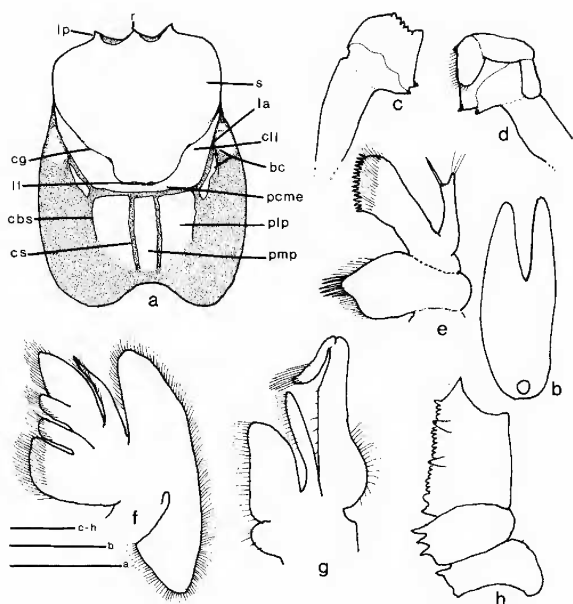


Figure 1. *Bythiopagurus macrocolus*, gen. nov., sp. nov.: a, ♂ paratype (6.4 mm), USNM 1007810; b–h, ♀ paratype (6.0 mm), J44760: a, cephalothorax; b, gill lamella; c, left mandible (internal view, palp removed); d, right mandible (internal view); e, left maxillule (external view, setal details omitted); f, left maxilla (external view, setal details omitted); g, left maxilliped 1 (external view, setal details omitted); h, coxa, basis and ischium of left maxilliped 3 (external view, setae omitted). Abbreviations: bc: branchiostegal areas of calcification; cbs: sulcus cardiobranchialis; cg: cervical groove; cll: carapace lateral lobe; cs: cardiac sulcus; la, linea anomurica; lp: lateral projection; lt: linea transversalis; pcme: posterior carapace median element; plp: posterolateral plate; pmp: posteromedian plate; r: rostrum; s: shield. Scales equal 1 mm (b–h) and 5 mm (a).

the linea transversalis. These calcified areas have now become incorporated into species descriptions as “accessory portion of the shield” (e.g. Asakura, 2001; McLaughlin and Lemaitre, 2001). Personal examination of the internal structure of the cephalothorax of *Propagurus depofundis*, *Porcellanopagurus tridentatus* Whitelegge, 1900, *Solitariopagurus triprobolus* Poupin and McLaughlin, 1996 and the new species have confirmed the structure and position of the linea transversalis as defined by Boas (1926) and Pilgrim (1973). The linea transversalis is a chitinous hinge separating the posterior portion of the shield from the median anterior portion of the posterior carapace. It does not curve anteriorly to delineate areas of calcification as illustrated by McLaughlin (1974: fig. 2), Lemaitre (1995: fig. 1), or McLaughlin and Lemaitre (2001: fig. 2); nor is it calcified as reported by McLaughlin (1997) and Asakura (2001). Although its position can be recognised externally, the linea transversalis itself often is not visible on the surface of the carapace and may be covered by a calcified plate.

In *Bythiopagurus macrocolus* gen. nov., sp. nov., the shield is completely delineated from the surrounding well calcified integument by the cervical groove (Fig. 1a), much as it is in the genera *Porcellanopagurus* Filhol, 1885 and *Solitariopagurus*

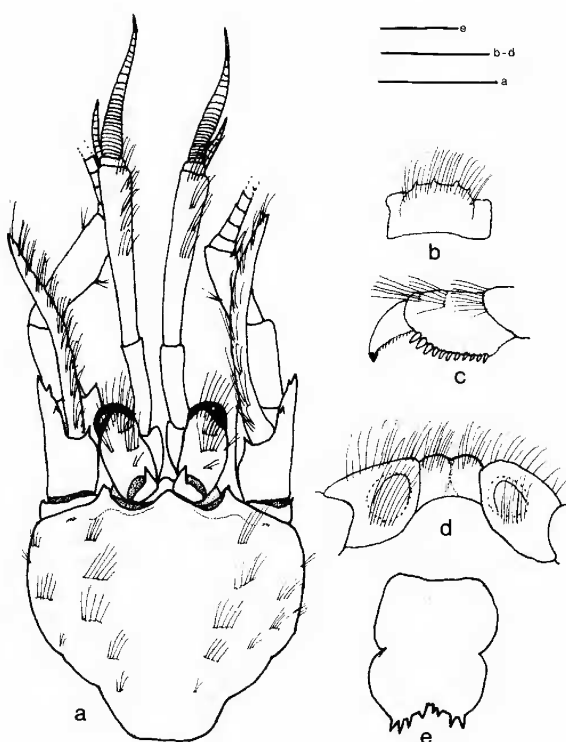


Figure 2. *Bythiopagurus macrocolus*, gen. nov., sp. nov.: a–d, ♂ paratype (6.4 mm), USNM 1007810; e, ♂ holotype (6.0 mm), J44765. a, shield and cephalic appendages (dorsal view, aesthetascs omitted); b, anterior lobe of sternite of pereopods 3; c, dactyl and propodus of left pereopod 4 (lateral view); d, coxae and sternite of pereopods 5; e, telson. Scales equal 3 mm (a), 2 mm (b–d) and 1 mm (e).

Türkey, 1986 (cf. McLaughlin, 2000: fig. 1). The linea transversalis in *B. macrocolus* is contiguous with the cervical groove centrally and delimits the calcified lateral elements posteriorly on either side of the posterior margin of the shield. In this respect, the linea transversalis of *B. macrocolus* is comparable to that of *Porcellanopagurus*, which directly abuts the posterior carapace lobes. However, the carapace is not broadened in *B. macrocolus* as it is in *Porcellanopagurus* and *Solitariopagurus*, thus the lateral calcified elements do not appear posterior as they tend to in the latter genera, particularly in *Solitariopagurus*. Nevertheless, these calcified elements cannot correctly be considered accessory portions of the shield, because by definition, the shield is delimited by the cervical groove (Forest, 1987: 18). Despite the positional homologies in the three genera, the anterolateral position of these calcified areas in *Bythiopagurus* necessitate that they be referred to as carapace lateral lobes (Fig. 1a) rather than posterior carapace lateral lobes. It would appear that these carapace lateral lobes are partially delimited anterolaterally by the linea anomurica, but these lineae are difficult to follow posteriorly in the membranous regions of the branchiostegites. Other terminology applied to the elements of the posterior portions of the

carapace follow those used by McLaughlin (2000) for *Porcellanopagurus* and *Solitariopagurus*.

***Bythiopagurus* gen. nov.**

Type species. Bythiopagurus macrocolus sp. nov.

Diagnosis. Shield and carapace lateral lobes well calcified; posterior carapace with posterior carapace element contiguous or fused with lateral carapace lobes, posteromedian and posterolateral plates also well calcified at least in anterior halves (Fig. 1a). Sulci cardiobranchialis extending approximately 0.50 length of posterior carapace; cardiac sulci extending nearly to posterior margin. Cervical groove distinct; linea transversalis usually partially discernable externally; linea anomurica not readily apparent in posterior portion of carapace. Frequently small areas of branchiostegal regions weakly calcified.

13 pairs of distally quadriserial (Fig. 1b) phyllobranchiate gills.

Ocular peduncles short and stout; ocular acicles acutely triangular. Antennal peduncles with supernumerary segmentation.

Mandibles sometimes weakly asymmetrical (Fig. 1c, d); strongly calcified; palp well developed. Maxillule (Fig. 1e) with anterior lobe of endopod weakly developed, posterior lobe moderately well developed, not recurved. Maxilla (Fig. 1f) with slender scaphognathite. First maxilliped (Fig. 1g) with slender two-segmented exopod; no epipod. Third maxilliped with basis and ischium not fused; crista dentata of ischium well developed (Fig. 1h), 1 or 2 accessory teeth.

Chelipeds subequal; left sometimes longer, but not stronger; dactyls and fixed fingers opening in horizontal plane. Fourth pereopod very weakly semichelate; propodal rasp consisting of single row of corneous scales (Fig. 2c). Fifth pereopod chelate. Male usually with papilla or very short sexual tube extruded from both right and left gonopores (Fig. 2d). Female with paired gonopores.

Abdomen somewhat reduced, dextrally twisted. Male with left unpaired pleopods on somites 3–5; exopods moderately long and very slender, endopods reduced. Female with paired and modified pleopod 1, unpaired left pleopods 2–4 with both rami of approximately equal length, endopods much thicker; pleopod 5 as in male.

Uropods markedly asymmetrical. Telson with transverse indentations; posterior lobes separated by median cleft; terminal margins each with few small spines.

Etymology. From Greek *bythios* meaning from the deep, and *pagurous* meaning crab, and referring to the archibenthic and archiabyssal depths from which the type species was collected.

***Bythiopagurus macrocolus* sp. nov.**

Figures 1–3

Paguridae n. gen. n. sp.—Koslow and Gowlett-Holmes, 1998: 30 (in part, see remarks).

Pagurid sp.—Poore, et al., 1998: 71 (in part, see remarks).

Material examined. Holotype. (6.0 mm), NMV J44765, CSIRO SS01/97 stn 41, 44°19.2'S, 147°07.2'E, 1083 m; 82.8 km SSE of SE Cape "U" seamount, Tasmania, Australia.

Paratypes. All from Tasmanian seamounts, collected on cruise CSIRO SS01/97. Stn 15, 82.9 km SSE of SE Cape "Sister 1",

44°16.2'S, 147°17.4'E, 1100 m, 23 Jan 1997, 6 (2.6–5.9 mm), 9 ♀ (3.2–6.4 mm), 5 ovigerous ♀ (4.2–6.2 mm), NMV J44760. Stn 28, 89.5 km SSE of SE Cape "K1", 44°17.4'S, 147°24.6'E, 1225 m, 25 Jan 1997, 4 (4.3–6.8 mm), 1 ovigerous ♀ (3.6 mm), NMV J44762. Stn 34, 85.4 km SSE of SE Cape "U", 44°19.8'S, 147°10.2'E, 1083 m, 27 Jan 1997, 3 ♀ (4.2–5.3 mm), NMV J44759. Stn 37, 84.0 km SSE of SE Cape "J1", 44°16.2'S, 147°19.8'E, 1300 m, 27 Jan 1997, 1 (4.9 mm), 1 ♀ (4.2 mm), 1 ovigerous ♀ (6.2 mm), NMV J44803. Stn 40, 82.6 km SSE of SE Cape "J1", 44°14.4'S, 147°21.8'E, 1200 m, 27 Jan 1997, 2 (4.4, 5.1 mm), 5 ♀ (5.1–6.4 mm), 5 ovigerous ♀ (sl = 5.1–6.3 mm), NMV J44758. Stn 41, 82.8 km SSE of SE Cape "U", 44°19.2'S, 147°07.2'E, 1083 m, 27 Jan 1997, 1 (4.2 mm), 1 ♀ (4.3 mm), 3 ovigerous ♀ (5.0–5.5 mm), NMV J44765; 2 (3.8, 6.4 mm), 1 ovigerous ♀ (5.3 mm), USNM 1007810. Stn 58, 81.2 km SSE of SE Cape "38", 44°13.2'S, 147°22.8'E, 1140 m, 30 Jan 1997, 1 (5.6 mm), NMV J44768. Stn 59, 81.6 km SSE of SE Cape "38", 44°13.8'S, 147°22.8'E, 1200 m, 30 Jan 1997, 1 (4.5 mm), NMV J44763. Stn 62, 87.8 km SSE of SE Cape "A1", 44°19.8'E, 147°16.2'E, 1200 m, 30 Jan 1997, 1 ovigerous ♀ (5.4 mm), NMV J44761.

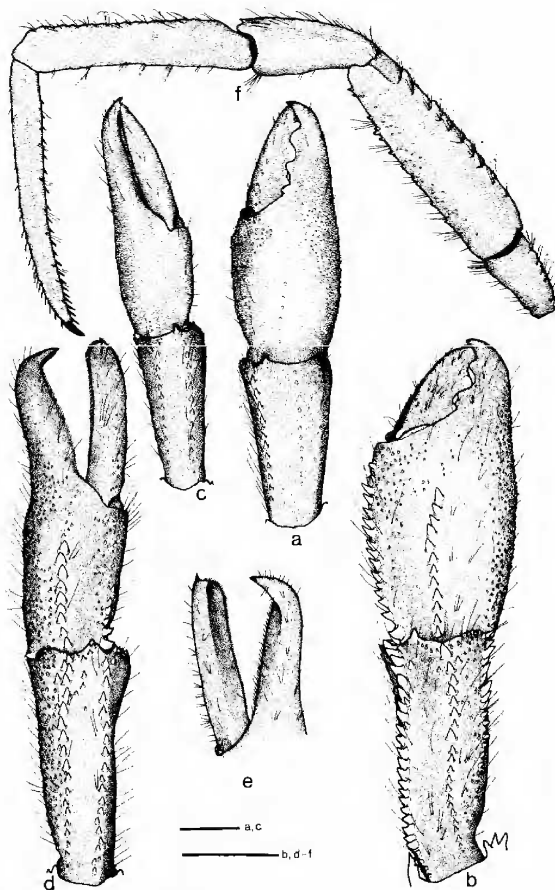


Figure 3. *Bythiopagurus macrocolus*, gen. nov., sp. nov.: a, c, ♂ paratype (2.6 mm), J44760; b, d–f, ♂ paratype (6.4 mm), USNM 1007810. a, b, chela and carpus of right cheliped (dorsal view); c, d, chela and carpus of left cheliped (dorsal view); e, dactyl and fixed finger of left chela (ventral view); f, left pereopod 2 (lateral view). Scales equal 5 mm (b, d–f) and 1 mm (a, c).

Other material examined. CSIRO SS91/97, no other data, 1 (5.6 mm), NMV J44801.

Description. Shield (Figs. 1a, 2a) broader than long; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin truncate; dorsal surface with numerous sparse tufts of simple setae. Rostrum triangular, reaching to or slightly beyond bases of ocular acicles; with or without terminal spinule. Lateral projections reaching level of rostrum or slightly beyond, each with prominent marginal or submarginal spine.

Ocular peduncles very short and stout, 0.40–0.50 length of shield; dorsal, mesial and lateral surfaces calcified, median longitudinal region of ventral surface membranous; dorsal surfaces of peduncles each with 3 or 4 short transverse rows of simple setae; corneas reduced dorsally by projection of peduncular integument, corneal diameter 0.40–0.50 of peduncular length. Ocular acicles each with slender triangular projection, terminating acutely and with small submarginal spine or spinule not usually visible dorsally; separated basally by approximately 0.50 basal width of 1 acicle.

Antennular peduncles overreaching distal margins of corneas by length of ultimate segments to nearly entire lengths of penultimate segments. Ultimate segments nearly twice length of penultimate segments, dorsal surfaces each with 3–5 short transverse rows of simple setae. Penultimate segments with few sparse tufts of setae. Basal segments each with slender spine on dorsolateral margin of statocyst lobe.

Antennal peduncles overreaching distal margins of corneas by entire lengths of fifth and fourth segments, but reaching only to approximately midlength of ultimate segments of antennular peduncles. Fifth and fourth segments with few sparse tufts of short setae. Third segment with spine at ventrodistal margin. Second segment with dorsolateral distal angle prominently produced, terminating in small spine and with 1 or 2 small spines on mesial margin; dorsomesial distal margin with well developed spine. First segment sometimes with spine on dorsolateral distal margin, ventrolateral margin with 1 spine. Antennal acicles reaching to or nearly to distal margin of fifth peduncular segment, terminating in small spine; mesial margin with row of sparse tufts of stiff setae.

Mandibles with upper incisor edge of left (Fig. 1c) with 2 to several calcareous denticles, cutting edge with corneous-tipped tooth at lower angle, sometimes also at upper angle, stout internal ridge presumably representing molar process with usually corneous-tipped tooth at lower angle; right mandible with upper edge of incisor process (Fig. 1d) unarmed or with 1 or 2 calcareous denticles, upper and lower angles of cutting edge each usually with corneous-tipped tooth, presumed molar process with usually corneous-tipped tooth at lower angle; palp three-segmented, distal segment with row of short marginal setae. Maxillule (Fig. 1e) with internal lobe of endopod not produced, but provided with 1 stiff bristle, external lobe somewhat produced, not recurved, with 3 terminal setae. First maxilliped (Fig. 1g) with setae of external margin of exopod only on proximal half. Third maxilliped (Fig. 1h) with prominent tooth at ventrodistal angle of coxa; basis with 2 or 3 spine-like teeth on ventral margin; ischium with well

developed crista dentata, usually 1 or occasionally 2 widely separated accessory teeth; merus and carpus each with dorsodistal spine.

Right cheliped (Figs 3a, b) long and slender. Dactyl 0.50 to nearly equal to length of palm; dorsomesial margin not delimited, rounded mesial face unarmed or with numerous minute spinules in proximal half; dorsal surface often with scattered small pits and individual or sparse tufts of short to moderately long setae; ventral surface with scattered tufts of longer setae; cutting edge usually with 2 or 3 large calcareous teeth, terminating in small corneous claw and slightly overlapped by fixed finger, occasionally crossed with fixed finger in larger specimens. Palm 0.70–0.95 length of carpus; armature of dorsomesial margin varying from ill-defined and irregular single or double row of small spinules or tubercles over entire length in small specimens to row of prominent spines in proximal 0.80–90 of margin and small spines or spinules in distal 0.10–0.20 in large individuals; dorsal surface with scattered very small tubercles or spinules, particularly in mesiodistal 0.35, dorsal midline with longitudinal row of 6–13 tiny to prominent spines, not extending to junction of dactyl and fixed finger; dorsolateral margin not delimited except faintly in some small specimens, but armed with numerous very small and tiny spinules, tubercles or granules, extending to distal 0–25–0.50 of fixed finger; mesial, lateral and ventral surfaces with tiny tubercles or spinules, sometimes forming short, transverse rows; surfaces all with scattered sparse tufts of short to moderately long setae, most numerous ventrally; cutting edge of fixed finger with 2 or 3 prominent calcareous teeth, calcareous ridge or sometimes few to several small calcareous teeth distally. Carpus slightly shorter to slightly longer than merus; dorsomesial margin with row of small to moderately prominent spines, dorsodistal margin usually with 1 small to large spine mesially and several very small spines laterally, occasionally only single small spine in small specimens; dorsal midline with row of small spines or spinules becoming row of prominent spines in large individuals, dorsolateral surface sloping, dorsolateral margin armed with weakly defined row of tiny spinules or tubercles in small specimens, increasing in size and number with increased body size; mesial and lateral faces each with scattered to moderately dense covering of very small tubercles or spinules, most numerous in small individuals, distal margins each sometimes with several spines or spinulose tubercles; ventromesial margin often tuberculate, ventral surface with scattered tubercles; ventrolateral margin usually not delimited, but with 1 or 2 spines at ventrolateral distal angle. Merus subtriangular; dorsal surface with row of short transverse ridges and sparse tufts of setae; mesial face with few sparse tufts of setae, ventromesial margin with row of conical, subacute spines, ventral surface often with scattered spines; ventrolateral margin not distinctly delimited but with short transverse rows of small tuberculate spines extending onto ventral surface. Ischium with row of small spines or spinules on ventromesial margin, ventral surface with few low protuberances or small spines and sparse setae. Coxa with spine on distal margin ventromesially and additional spine ventrolaterally.

Left cheliped (Figs 3c–e) often as long as or slightly longer than right; dactyl approximately 0.50 longer than palm; dorsal

surface slightly elevated proximally, dorsomesial margin not delimited, but with transverse tuberculate or minutely spinulose ridges and sparse setae, few spinules on dorsal surface in proximal half, dorsal surface also with scattered stiff setae; cutting edge with row of small corneous spines, rounded tip of dactyl slightly overlapped by corneous claw of fixed finger (Fig. 2c) in small specimens (e.g. 2.6 mm), just beginning to show overlap by fixed finger (e.g. ovigerous ♀ 3.6 mm), or completely overlapped by hooked end of fixed finger (Figs 2d, e) in large specimens (e.g. 3.5 mm, ♀ 5.0 mm); inner surface of dactyl concave, small corneous claw laterally positioned at tip of dactyl. Palm 0.65–0.80 length of carpus; dorsomesial margin variable: not delimited in small specimens, but rounded surface frequently armed with numerous tiny spinulose tubercles or small spines often increasing in size proximally and tufts of setae; large specimens with well delimited margin armed with row of small spines not quite extending to distal margin, 1 or 2 prominent spines at proximal angle; dorsal surface elevated in midline and armed with row of 3–11 minute to moderately prominent tuberculate spines, not reaching to articulation of dactyl, but often continued as irregularly-set very small spinules in large individuals; dorsomesial surface unarmed in small specimens, but with increasing number of small or very small spinules with increased size, primarily in distal half; dorsolateral surface sloping and armed with numerous minute to small spinules and/or tubercles, continued onto proximal half of fixed finger, dorsolateral margin varying from well delimited by row of small spines to not delimited, but rounded surface with numerous tiny to small spinules or spinulose tubercles also continued onto fixed finger but not extending to tip, dorsolateral proximal angle with blunt tubercle or spine; ventral surface with small spinules or spinulose tubercles laterally, remainder of ventral surface with tufts of sparse setae; distal portion of fixed finger curved and slightly overlapping dactyl in small specimens, but becoming drawn out into hook-like tip with increased size, terminating in small corneous claw; inner surface of fixed finger oblique in small individuals to prominently concave, particularly distally in larger specimens. Carpus slightly shorter to approximately equal to length of merus; dorsodistal margin with 1 to several small spines; dorsomesial margin with irregular row of small to moderately large spines, dorsal surface often with few small spines, at least distally and tufts of sparse setae, irregular row of small to moderately large spines beginning proximally at dorsolateral angle but becoming almost median distally in larger specimens because of sloping dorsolateral surface; in smaller specimens lateral face tending to be more perpendicular, surface armed with numerous tiny to small spinules or tubercles, ventrolateral margin delimited by row of small spines or simply rounded with surface armature continued onto ventral surface laterally; mesial face with scattered tufts of sparse setae, distomesial margin and mesial surface ventrally spinulose or tuberculate; remainder of ventral surface with few low protuberances and tufts of sparse setae. Merus subtriangular; dorsal surface with short transverse rows of sparse setae; ventromesial margin with row of irregularly-sized spines; ventrolateral margin with row of somewhat smaller spines, lateral face ventrally with short transverse rows of very small tubercles or granules accompanied by tufts of setae;

ventral surface with few small spines, particularly laterally, and scattered tufts of sparse setae. Ischium with row of small spines on ventromesial margin, 1 small spinule on ventrolateral margin distally, ventral surface occasionally with few scattered small spines. Coxa with spine on ventromesial distal margin and additional spine on distal margin ventrolaterally.

Ambulatory legs (Fig. 3f) similar from left to right, usually only slightly overreaching tips of chelipeds, if at all. Dactyls 0.10–0.30 longer than propodi; dorsal surfaces each with row of tufts of moderately short sparse setae, interspersed with corneous spinules in distal 0.25–0.45; lateral faces generally flattened, each with faint longitudinal sulcus flanked dorsally and ventrally by row of sparse setae; mesial faces each with weak longitudinal sulcus and row of corneous spinules dorsally; ventral margins each with row of 15–23 corneous spines; terminating in sharp corneous claw. Propodi 0.50–0.70 longer than carpi; dorsal surfaces each with low protuberances and numerous tufts of sparse setae; lateral faces each usually with row of tufts of sparse setae dorsally; ventral surfaces each with few tufts of sparse setae, 1 or 2 corneous spines on each ventrodistal margin, at least on second. Carpi each with small dorsodistal spine; dorsal surfaces with few low, occasionally weakly spinulose, protuberances and tufts of sparse setae; lateral faces each with row of sparse setae dorsally; ventral surfaces each with 2 or 3 tufts of setae. Meri each with transverse ridges and sparse setae dorsally; ventral margins of second pereopods each with irregular row of small spines and tufts of sparse setae, lateral faces often with few to numerous spinules or granules in lower half; third with ventral margins usually unarmed, rarely with few minute spinules or granules, but with scattered tufts of setae. Ischia each with dorsal and ventral tufts of setae. Anterior lobe of sternite of third pereopods (Fig. 2b) subrectangular, anterior margin with 1 or 2 pairs of small subacute or acute spines.

Telson (Fig. 2e) with posterior lobes symmetrical or only weakly asymmetrical; terminal margins somewhat oblique, each armed with 1 or 2 to several spines.

Colour (in preservative). Cephalothorax and appendages all generally orange to reddish-orange.

Reproduction. Slightly more than half of the females collected were ovigerous, but few if any of the eggs were near to hatching (eyed). The eggs were relatively small (diameter 0.75–0.98 mm) and quite numerous, although precise counts were not possible because of obvious loss during preservation and transport.

Variation. Variation in shape and armature of the chelipeds is appreciable in *B. macrocolus* as is indicated in the description, and this appears to be a function of size rather than sexual dimorphism. Small specimens of both sexes do not have the prominent spines on the dorsomesial margin of the right chela (Fig. 3a) or on the dorsomesial margins of the right and left carpi seen in large specimens. Similarly, the median row of spines on the right chela becomes increasingly more pronounced with increasing animal size. In contrast, the row of spines often delimiting the dorsolateral margin of the chela of the right in small individuals becomes indistinguishable in larger specimens. The very unusual development of the dactyl

and fixed finger of the left cheliped may be an adaptation to its distinctive environment; however, it is unquestionably correlated with animal growth. In the smallest specimen (♂2.6 mm) the corneous claw of the fixed finger overlaps the rounded tip of the dactyl (Fig. 3c) but the terminal portion of the fixed finger has not yet developed into a hook. The ventral surfaces of the dactyl and fixed finger, while sloping inward in this small male, do not exhibit the prominent concavities seen in larger individuals (Fig. 3e). Although these morphological variations are seen in both sexes, there appears to be a developmental "lag" in females. In males and females of similar size, spination on the dorsomesial margins of chela and carpi tends to be more prominent in males, whereas the loss of marginal distinction dorsolaterally on the chela occurs more rapidly.

Distribution and habitat. Seamounts U, J1, K1, A1, 38 and Sister 1 off south-eastern coast of Tasmania; 1083–1300 m; typically occupying small gastropod shells; found in association with primarily dead colonies (Gowlett-Holmes, 1998: 47) of stony coral, *Solenosmilia variabilis*.

Etymology. From Greek *makros*, meaning long, and *kolon* meaning leg, and indicative of the long-leggedness of this hermit crab.

Remarks. Because size-related diagnostic characters are not apparent in small specimens, individuals of shield lengths <2.8 mm, particularly females, *Goreopagurus poorei* Lemaitre and McLaughlin, 2003 look superficially like small *B. macrocolus*. Consequently, specimens reported by Koslow and Gowlett-Holmes (1998: 21) from "Andys" and "Main Pedra" seamounts and Poore et al. (1998: 77) from stations 03, 06, and 56 were incorrectly referred to *B. macrocolus*. Two lots, one from "Andys" (stn 56) and one from "Main Pedra" (stn 03), are *G. poorei*. The single female (4.2 mm) from "Main Pedra" seamount (stn 06) belongs to *Pagurodes inarmatus* Henderson, 1888, which shares with the aforementioned species distinctly shortened ocular peduncles.

The majority of specimens of *B. macrocolus* had been removed from their shells shortly after capture but a few examined still occupied shells. These shells were worn and frequently damaged but the most notable observation was that the shells rarely even completely covered the abdomens of the crabs. Correspondingly, there appeared to be reduction in overall abdomen length with increased animal size. The need for only minimal abdominal protection is undoubtedly correlated with the appreciable calcification of the cephalothorax of *B. macrocolus* as it is in species of *Labidochirus* Benedict, 1892, *Porcellanopagurus*, and *Solitariopagurus*. Whether a similar correlation exists between abdomen length and shell size cannot be adequately determined from the limited material.

Discussion

Certain morphological characters shared by *Bythiopagurus* and *Icelopagurus* McLaughlin, 1997 might suggest a relationship between the two. Both monotypic genera are defined as having broad, well calcified anterior carapaces, very short ocular peduncles, long antennular and antennal peduncles and elongate chelipeds and ambulatory legs. However, that the similar-

ities are superficial and not phylogenetic is clearly apparent when gill number and structure, mandibular and maxillary development, male and female secondary sexual characters and telsonal structure are considered. *Bythiopagurus* has 13 pairs of distally quadriserial gills, whereas *Icelopagurus* has 11 biserial pairs. The mandibles, or at least the left, has a denticulate upper margin in *Bythiopagurus*, while this margin is smooth in *Icelopagurus*. The external lobe of the endopod of the new genus is produced but it is rudimentary or vestigial in *Icelopagurus*. Papillae or very short male sexual tubes usually are produced from both gonopores in *Bythiopagurus* but the right sexual tube in *Icelopagurus* is of moderate length (> 2 coxal lengths) and directed toward the exterior. Females of the new genus have pleopod 1 paired and modified; no first pleopod development occurs in females of *Icelopagurus*. The very distinctive telson, which is armed on the terminal margin of each posterior lobe with several long corneous spines sets *Icelopagurus* apart from all other genera.

Papillae or paired, very short sexual tubes, paired and modified female pleopod 1, quadriserial gill structure, development of the external lobe of the endopod of the maxillule, short stout ocular peduncles, and subequal chelipeds are characters that *Bythiopagurus* shares with *Michelopagurus* McLaughlin, 1997, and these characters certainly might suggest more than a superficial relationship. That the gills are only distally divided in the new genus and deeply divided in the latter genus is of little significance. McLaughlin and de Saint Laurent (1998) found that gill lamellae in their genus, *Propagurus*, varied from biserial to distally quadriserial within a single gill of *P. deprofundis*. Lemaitre (2003b) has shown that in species of *Sympagurus* Smith, 1883 considerable variation occurs in the extent of lamellar division, both within and among species. More important is the fact that there are 13 pairs of gills in *Bythiopagurus*, but only 11 in *Michelopagurus*. Other characters also indicate that the observed similarities most probably are convergent. Perhaps most significant are the major differences in cephalothoracic calcification among species of the two genera, the dentition on the mandible(s) in *Bythiopagurus*, and the lack of fusion between the basis and ischium of the third maxilliped in the latter genus.

De Saint Laurent-Dehancé (1966) considered those few genera of Paguridae that have 13 pairs of gills to be the most primitive genera. At the time of her report, only five genera, *Munidopagurus* A. Milne-Edwards and Bouvier, 1893, *Xylopagurus* A. Milne-Edwards, 1880, *Pylopaguropsis* Alcock, 1905, *Tomopaguropsis* Alcock, 1905, and *Tomopaguroides* Balss, 1912, were included in her *Pylopaguropsis*-group although she was aware of additional undescribed genera. In addition to gill number, this group of genera was characterised by the presence of an accessory tooth on the crista dentata of maxilliped 3, by paired first and/or second pleopods in males or paired pleopod 1 in females, but with males lacking sexual tubes.

Since de Saint Laurent-Dehancé's (1966) discussion of relationships among genera of Paguridae, an additional 41 genera have been described, of which only five can be included in her *Pylopaguropsis*-group: *Lithopagurus* Provenzano, 1968, *Bathypaguropsis* McLaughlin, 1994, *Propagurus*, *Chano-*

pagurus Lemaître, 2003a, and *Bythiopagurus*. All have 13 pairs of gills but pleurobranchs of the fifth and sixth thoracic somites (cephalothoracic somites XI and XII, McLaughlin and Lemaître, 2001) are reduced or rudimentary in *Chanopagurus* and *Propagurus*. De Saint Laurent-Dehancé (1966: 259) was of the impression that all genera in the *Pylopaguropsis*-group had quadriserial gills but Asakura (2000) has demonstrated that the gills in species of *Pylopaguropsis* are really biserial. The gills in *Lithopagurus* and *Munidopagurus* are also reported to be biserial (McLaughlin, 2003). Lemaître (1995) had described the gills of *Xylopagurus* as biserial whereas McLaughlin (2003) indicated that both bi- and quadriserial gills occurred in species of that genus. Lemaître (pers. comm.) has now found that gills in species of *Xylopagurus* vary from very weakly divided distally (practically biserial) to distally divided (quadrise-rial).

With the exception of *Tomopaguroides* where the crista dentata has not been described, all have an accessory tooth; however, there may be one or two teeth in *Bythiopagurus*. The mandible has been described as having a denticulate upper margin only in *Bythiopagurus* and *Pylopaguropsis* but in the former genus, the incisor process usually is provided with small corneous-tipped teeth. A truly corneous-toothed incisor process has been described only in the Pylojacquesidae McLaughlin and Lemaître, 2001 but even calcified individual teeth are rare in Paguroidea.

Males of *Xylopagurus* have both pleopods 1 and 2 paired, whereas only pleopod 2 is paired in *Lithopagurus* and *Tomopaguroides*. Males of *Chanopagurus* are unknown, but in none of the remaining six genera are either pleopods 1 or 2 paired, although unpaired pleopods may or may not be present. Contrary to de Saint Laurent-Dehancé's (1966) diagnosis of the *Pylopaguropsis*-group, males of *Bythiopagurus* do have extruded papillae or very short sexual tubes. As noted by Lemaître and McLaughlin (2003), whether the presence of very short sexual tubes or simple papillae reflects an early stage in evolutionary sexual tube development or is a function of sexual activity in species lacking sexual tube development is not known. Paired female gonopores are characteristic of the *Pylopaguropsis*-group but females of *Chanopagurus* have a single left gonopore. Paired pleopod 1 occurs in females of several genera, but not in *Bathypaguropsis*, *Lithopagurus*, *Propagurus*, or *Tomopaguropsis*. Females of *Tomopaguroides* are unknown.

Clearly, the presence of 13 pairs of gills is the single unifying character of the *Pylopaguropsis*-group, as in virtually all other morphological attributes there is extreme diversity. However, for the four genera of the group in which some larval information is available, Provenzano (1971) commented that the several unusual features found in the zoeas of *Pylopaguropsis atlantica* Wass., 1963, *Lithopagurus yucatanicus* Provenzano, 1968, *Munidopagurus macrocheles* (A. Milne-Edwards, 1880), and *Xylopagurus rectus* A. Milne-Edwards, 1880 could not be without phylogenetic significance.

McLaughlin and de Saint Laurent (1998) noted that species of *Propagurus* exhibited morphological variations that suggested this genus was undergoing evolutionary transformations from those of the typical *Pylopaguropsis*-group genera to those seen in *Pagurus*-like genera. In addition to the overall develop-

ment of gill lamellae that varied from deeply quadrise-rial to only distally divided, these authors pointed to reduction in the pleurobranch of the fifth thoracic somite and to the develop-ment of the external lobe of the maxillary endopod, which varied from well developed to rudimentary. If the other mor-phological variations demonstrated among genera of the *Pylopaguropsis*-group are considered in a similar context, it might be possible to develop a model of evolutionary change using this small, and presumably monophyletic, potentially primitive group of pagurids that would be applicable to the larger conglomerate of taxa with 11 or fewer pairs of gills.

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